Review

Kaolin, an emerging tool to alleviate the effects of abiotic stresses on crop performance

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ABSTRACT

In the context of climate change, the combination of the drought, salinity, heat and high irradiance felt in many regions around the world will be intensified, further worsening the adverse effects on plant growth and development at different scales. This scenario will have severe repercussions on agricultural crops, compromising yields and harvest qualities. Kaolin (KL) clay has been recognized as a promising short-term strategy for the sustainable alleviation of adverse abiotic stress. However, some mechanisms that support KL-induced stress alleviation remain minimally discussed, and there is still no consensus on its effectiveness in different crops and under different stress prevalences and/or intensities. Based on most available reports, this review illustrates KL's modes of action and critically appraises crop responses to KL application, namely, its influence on temperature, irradiation reflection, leaf structure, water status, photosynthetic capacity, biochemical responses, mineral composition, growth, yield and quality. Finally, this review briefly highlights some less explored aspects that merit attention.

1. Introduction

Impacts from recent climate-related extremes, such as heat waves, droughts, floods, cyclones, and wildfires, have revealed the significant vulnerability and exposure of some agro-ecosystems to the current climate variability. Furthermore, the forecasted scenarios are even more worrisome, demonstrating rises in global temperatures, which are more marked during the night, changes in precipitation patterns and increases in the intensity and frequency of extreme events (IPCC, 2013).

In many regions of the globe, typical stresses include drought, salinity, an excessive heat load and high daily irradiance (both photosynthetic active radiation, PAR, and ultraviolet radiation, UV). Drought, salinity, heat and high irradiance stresses are considered some of the most limiting factors for agricultural productivity worldwide, exhibiting synergistic effects with concomitant consequences on growth, productivity and harvest quality. Drought has negative repercussions on water relationships, nutrient uptake, carbon assimilation, respiration, hormone levels and oxidative pathways (Farooq et al., 2009; Brito et al., 2018a,b). Increased soil and water salinization expose plants to the adverse effects of salinity. Although plant responses to drought and salinity are often similar, in the latter stress type, the developed osmotic stress is followed by ion toxicity, causing a disruption of cellular organelles and their metabolism (Bosco de Oliveira et al., 2013). Moreover, in addition to the exacerbated drought and salinity effects, high temperatures also influence membrane stability and protein denaturation and aggregation (Wahid et al., 2007). Additionally, under high photosynthetic photon flux density (PPFD), transpiration, respiration and photorespiration rates are altered in plants, and photoinhibition and chlorosis are observed (Moutinho-Pereira et al., 2009). The high levels of ultraviolet-B radiation also induce deleterious morphological, physiological and biochemical changes (Correia et al., 2005).

In this sense, agronomic strategies must be implemented to maintain and improve the sustainability and competitiveness of agronomic crops subjected to these stressors. There are a large number of potential adaptations for cropping systems that could be implemented to cope with the adverse conditions, such as the use of more tolerant rootstocks and cultivars, the implementation of breeding programmes, changes in orchard design and canopy management, adoption of efficient irrigation strategies, improvement of soil management, and application of specialty protector compounds. Given the high natural limitations in water resources and rugged topography of some arid and semi-arid areas of the globe, large-scale systems of water captation and distribution involve high costs and are environmentally unsustainable. By contrast, attempts to improve tolerance through plant breeding methods are time-consuming and laborious, relying on the existing

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genetic variability (Kaya et al., 2009); additionally, the modification of single traits is difficult due to the likelihood of multigene control. Therefore, without disregarding the importance of irrigation and genetics in improving crop performance under stress conditions, it is crucial to act on short-term adjustments. In this review, we highlight the use of kaolin in crop abiotic stresses alleviation. Initially, kaolin (KL) was formulated to function in pest control (Glenn and Puterka, 2005), but its use in the mitigation of some environmental stresses has been increasingly studied in recent years. Its effectiveness is related to the white protective particle film that is formed on leaves surface, which increases the reflection of excess radiation, reducing the risk of leaf and fruit damage due to heat load accumulation and solar injury (Glenn and Puterka, 2005; Glenn, 2012). However, although KL has been studied in a large number of species, namely, in fruit trees, the plant-induced changes are still not fully understood. In addition, there remains no consensus concerning its effectiveness in different crops and under different stress prevalences and/or intensities (Denaxa et al., 2012; Boari et al., 2015; Nanos, 2015; Brillante et al., 2016; Dinis et al., 2016a; Brito et al., 2018c). The characterization and mode of action, as well an overview of the effects of KL on crop performance, are extensively reviewed by discussing the interactive effects on morphological, physiological, biochemical, growth, yield and harvest quality responses.

2. Kaolin characterization and effect on abiotic stresses alleviation

KL ($Al_2Si_2O_5(OH)_4$) is a white mineral that is chemically inert, non-abrasive, non-toxic and easily disperses in water. Once sprayed as a suspension on the leaf surface, water evaporates to leave a protective particle film (Cantore et al., 2009; Glenn and Puterka, 2005). Produced via particle film technology, KL consists of a combined synthesis of knowledge on mineral technology, insect behaviour, and light physics applied to pest control and plant physiology (Glenn and Puterka, 2005). KL is formulated as a wettable powder for application with conventional spray equipment. The KL particle film increases the reflection of excess radiation, including photosynthetically active (PAR), ultraviolet (UV) and infrared radiation (IR), reducing the risk of leaf and fruit damage from heat load accumulation and solar injury (Glenn, 2012; Glenn and Puterka, 2005). To obtain the desired results on plant tissues, an effective particle film must have certain characteristics. In particular, the mineral particle must have a diameter < 2 μm, must be formulated to spread and create a uniform film, should transmit PAR but exclude UV and IR radiation to some extent, should not interfere with gas exchange from plant organs, must alter insect/pathogen behaviour on the plant, and, of fundamental importance, must be removable from harvested commodities (Glenn and Puterka, 2005; Sharma et al., 2015). Moreover, kaolin should be applied before the occurrence of pests or high temperature and must be reapplied to protect new growth or after a heavy rain (Sharma et al., 2015).

Interestingly, recent evidence has revealed an added benefit of kaolin, the potential mitigation of elevated ozone levels, and effect that is positively related to air temperatures (Glenn, 2016). According to the author, kaolin particles also catalyses the degradation of ozone and increase the surface area in the particle film to provide a habitat for microbial populations, which may further facilitate ozone degradation on plant surfaces.

3. Kaolin effects on crops

The effects of KL on leaf and canopy temperatures, gas exchange, metabolic processes, growth, yield and plant product quality are not yet fully understood. In fact, they depend on several factors that may act in combination or in isolation: (i) applied concentration, as a high concentration reduces the availability of PAR (Rosati et al., 2006; Wünsche et al., 2004; Shellie and King, 2013); (ii) plant species and cultivars

(Glenn et al., 2005; Shellie and Glenn, 2008; Glenn, 2009; Roussos et al., 2010; Denaxa et al., 2012); (iii) environmental conditions, as KL typically improves plant performance under harsh conditions, when plants cannot use all the PAR that reaches the leaves (Jifon and Syvertsen, 2003; Glenn, 2009; Denaxa et al., 2012; Boari et al., 2015; Brillante et al., 2016; Brito et al., 2018c, 2019); (iv) the dimensions of the canopy/plant age, as different responses are expected in open compared with dense canopies, related with changes in light distribution within the canopy and the amount of carbon consumed during the respiration process (Rosati et al., 2007; Cantore et al., 2009; Glenn, 2009; Brito et al., 2018a) and (v) duration of the experiments, as in long-term studies, the influence of the variation of factors iii and iv is higher, and the capacity to develop resistance mechanisms against stress factors may be different, including the recovery capacity, leading to dissimilar results (Shellie and Glenn, 2008; Nanos, 2015).

3.1. Temperature and irradiation reflection

KL particle film technology has been tested as a tool to save water and improve crop performance since it can alter the microclimate around sprayed leaves. Some studies have demonstrated an effect of KL on solar radiation reflection (Rosati et al., 2006, 2007; Shellie and King, 2013; Nanos, 2015). For instance, an increase of 86% in PAR reflection from KL-sprayed (5% w/v) olive trees has been reported (Nanos, 2015), and KL (6%) increased leaf whiteness in 62% and reduced PAR transmittance by 28% in grapefruit trees (Jifon and Syvertsen, 2003). As the formed film not only reflects PAR and UV but also IR (Brillante et al., 2016), and despite some exceptions under specific conditions, the reduction of the KL-sprayed organ temperature is a general event. For instance, KL was found to reduce the leaf/canopy temperature in almond trees (Rosati et al., 2006), apple trees (Glenn, 2009, 2016), olive trees (Denaxa et al., 2012), grapevines (Correia et al., 2014; Brillante et al., 2016), tomato (Boari et al., 2015; AbdAllah, 2017) and gooseberry plants (Segura-Monroy et al., 2015). Similarly, sprayed fruits also showed lower surface and/or inner temperatures, as described for apple (Glenn et al., 2002), pear (Colativa et al., 2011) and tomato (Pace et al., 2007; Cantore et al., 2009; AbdAllah, 2017). Thus, the reduction of the leaf-to-air vapour pressure deficit ($VPD_{leaf-air}$) is also a regular effect (Jifon and Syvertsen, 2003; Glenn and Puterka, 2005; Rosati et al., 2006).

3.2. Water status and leaf structure

The KL particle film also has repercussions on water relationships and leaf structural characteristics. In general, the improvement of plant water status is a general effect of KL application in stressed plants (Glenn et al., 2010; Denaxa et al., 2012; Boari et al., 2015; Nanos, 2015; AbdAllah, 2017; Dinis et al., 2018; Brito et al., 2018c, 2019). Nevertheless, some different results may be obtained under specific conditions. For instance, AbdAllah (2017) described no effect on the relative water content (RWC) of KL-sprayed tomato plants under both favourable water and severe stressful conditions, while RWC was improved under moderate drought conditions. By contrast, the RWC of young potted olive trees was only improved under severe stressful conditions (Brito et al., 2018c), while the positive effect of KL in RWC of rainfed field olive trees was lost under more severe summer stress conditions (Brito et al., 2019). By contrast, under salinity conditions, the water potential of tomato plants was improved by KL, namely at a higher stress level (Boari et al., 2015). These results suggest that the efficiency of KL in improving plant water status was strictly related to the stress severity tolerance of each plant, and it was eventually lost when conditions became extremely severe. Consistently, higher succulence is also common in KL-sprayed leaves (Denaxa et al., 2012; Brito et al., 2018c). This ability to maintain turgid leaves has several physiological advantages, especially in drought environments, allowing the maintenance of turgor-dependent processes such as growth, stomatal activity
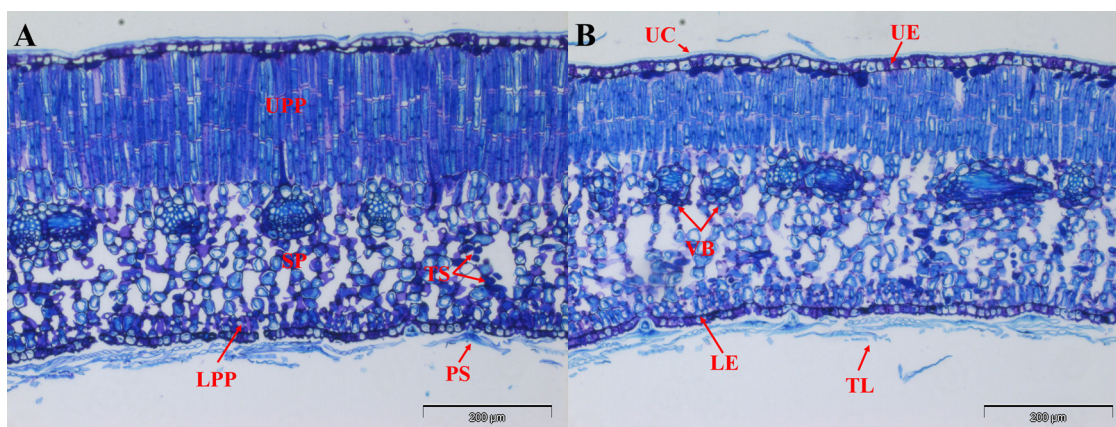
Fig. 1. Light microscopy images of olive leaf transversal sections stained with toluidine blue. Control (A) and Kaolin (B) treatments. Abbreviations: UC = upper cuticle; UE = upper epidermis UPP = upper palisade parenchyma; SP = spongy parenchyma; LPP = lower palisade parenchyma; VB = vascular bundles; TS = trichoscutereids; LE = lower epidermis; TL = trichome layer; PS = peltate scales (After Brito et al., 2019) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

and photosynthesis (Mullan and Pietragalla, 2011).

Kaolin may counteract the effect of water shortage and high irradiation on leaf sclerophylly and structural traits, as illustrated in Fig. 1. KL-sprayed leaves displayed a lower density and thickness (Denaxa et al., 2012; Segura-Monroy et al., 2015; Brito et al., 2018c, 2019) as well leaf mass area (LMA) (Nanos, 2015). Moreover, olive leaves showed a reduced thickness that was essentially due to a thinner upper palisade parenchyma, which in turn contributes to reducing the palisade/spongy parenchyma ratio (Brito et al., 2018c, 2019), indicating a less compact arrangement of mesophyll cells (Bacelar et al., 2004) and a reduced necessity to restrict water loss (Brito et al., 2019). In addition, a reduced density of trichomes has also been reported in olive tree and cape gooseberry leaves (Segura-Monroy et al., 2015; Brito et al., 2019). This response also reveals a reduced necessity for protection, as plants usually increase leaf pubescence to restrict radiation interception and water vapour diffusion (Bacelar et al., 2004; Glenn and Puterka, 2005; Bacelar et al., 2009) and to increase water-use efficiency by increasing leaf boundary-layer resistance (Savé et al., 2000). In addition, a reduced cuticle has been reported in KL-sprayed olive leaves, which resulted in increased cuticular transpiration (Brito et al., 2018c).

Stomatal density was also found to be affected by KL application and was higher in rainfed olive trees (Brito et al., 2019) and drought-exposed cape gooseberry plants (Segura-Monroy et al., 2015) sprayed with kaolin. As stomatal density was found to increase under moderate drought, followed by a decrease with increasing drought severity (Xu and Zhou, 2008), and to decrease with a higher temperature (Beerling and Chaloner, 1993), the drought and heat stress alleviation induced by KL application might contribute to the higher stomatal density. This response is of great ecophysiological relevance because higher stomatal densities improve the stomatal regulation capacity, increasing the ability to balance water loss with photosynthetic performance (Casson and Gray, 2008).

3.3. Gas exchange and photosynthetic responses

Kaolin spray largely influences leaf gas exchange and photochemistry responses. Under optimal hydration, KL usually decreases the stomatal conductance (g_s) and net photosynthetic rate (A) (Cantore et al., 2009; Boari et al., 2014, 2015). Similarly, during rewatering events after drought episodes, particularly under low irradiance and rainy weather conditions, the restauration of gas exchange variable was delayed by KL film (Brito et al., 2018a). Under all these conditions, the low light intensity promoted by kaolin may prevail, leading to a reduction of g_s and A (Gregoriou et al., 2007; Denaxa et al., 2012; Brito et al., 2018c). By contrast, in water-limited environments, salinity, high

temperature, high PPFD and/or large VPD, g_s and A were found to be positively influenced by KL in grapefruit trees (Jifon and Syvertsen, 2003), apple trees (Glenn, 2009; Glenn et al., 2003), grapevines (Correia et al., 2014; Dinis et al., 2018), tomato (Boari et al., 2014, 2015), olive trees (Denaxa et al., 2012; Nanos, 2015; Brito et al., 2018c, 2019) and mango trees (Chamchaiyaporn et al., 2013). Nonetheless, KL-sprayed leaves appear to need a period of acclimation to benefit from KL application (Brito et al., 2019). Apart from the dependence on g_s, as reported above, the improvement in photosynthetic activity in KL-treated leaves is also associated with the preservation of photosynthetic machinery integrity, as confirmed by chlorophyll a fluorescence traits in grapevines (Correia et al., 2014; Dinis et al., 2016a, 2018), grapefruit trees (Jifon and Syvertsen, 2003), olive trees (Brito et al., 2018c, 2019) and cape gooseberry (Segura-Monroy et al., 2015). Interestingly, as described for olive tree under rainfed field conditions, gas exchange variables during restauration were not only accelerated after the first rains, but they also persisted above control values during the autumn and winter months, when the KL film was no longer visible (Brito et al., 2019). Overall, these studies support the theory that the benefits of KL on photosynthetic capacity mainly occur under harsh conditions, when plants cannot utilize all the radiation that reaches the leaves, while KL can decrease the photosynthetic rate when environmental conditions limit photosynthesis, such as under low PPFD. However, other studies have shown a bit more complex picture. In different olive cultivars under similar drought conditions, KL did not affect g_s and increased A in one genotype (Denaxa et al., 2012), while it increased g_s and slightly decreased A in another cultivar (Roussos et al., 2010). Moreover, in walnut and almond trees, the reduction in temperature and VPD$_{leaf-to-air}$ promoted by KL were not sufficient to minimize the adverse effects in A, despite the absence of an influence on g_s (Rosati et al., 2006). A loss of KL effectiveness has also been described in terms of maintaining both g_s and A under severe stress conditions, both in olive trees (Nanos, 2015; Brito et al., 2018c, 2019) and grapevines (Shellie and Glenn, 2008). In agreement with these findings, in grapevines, Brillante et al. (2016) reported a negative influence of KL during years of high stress and the absence of an influence during less stressful years. These outcomes may suggest that, in addition to the specificity of each species and cultivar, the effectiveness of KL in the mitigation of stress effects on leaf gas exchange variables is higher under moderately stressful conditions and may be compromised with stress prevalence and/or intensity.

Despite the function of KL as an antitranspirant, few studies assessing the leaf transpiration rate (E) revealed that KL could induce an increase in g_s to a greater extent than in E (Correia et al., 2014; Boari et al., 2015; Brito et al., 2018c). A possible explanation may be provided by the reduced VPD$_{leaf-air}$ (Jifon and Syvertsen, 2003; Rosati

et al., 2006), which can reduce the driving force for transpiration while possibly promoting an increase in g_s (Zhang et al., 2017). Conversely, Brito et al. (2018c) observed that during the night, g_s and, consequently, E of drought-exposed olive trees were repressed by the application of KL, as the leaf water losses were essentially due to cuticular transpiration, whereas in control plants, they had a greater relationship with stomatal transpiration. As a result, whole-plant transpiration during the night accounted for 8.6% of the whole-day transpiration in KL plants versus 21% in control plants. Simultaneously, KL plants displayed a higher respiration rate, demonstrating an increased capacity to maintain normal metabolism (Brito et al., 2018c).

Interestingly, in some cases, although KL might affect negatively A at the leaf scale, this phenomenon was not reflected in photosynthesis on the whole-canopy scale and/or in plant biomass accumulation. For instance, concomitant with a decrease in photosynthesis at the leaf scale, Roussos et al. (2010) described an increase in the canopy dry weight of young olive trees, Rosati et al. (2007) observed an increase in whole-canopy photosynthesis of almond and walnut trees, and Wünsche et al. (2004) found no influence on whole-canopy photosynthesis of apple trees. These results resulted from the ability of KL to alter the light distribution within the canopy, increasing the incident radiation on inner canopy leaves, which were previously shaded or partially shaded. Thus, the reduction of PPFD at the leaf level was compensated, resulting in an increased carbon gain at the whole-plant scale (Rosati et al., 2007; Glenn, 2009). However, this phenomenon can be more evident in trees with large three-dimensional canopies. For instance, Cantore et al. (2009) found a reduction in A at the canopy scale in tomato plants, probably because the architecture of the canopy from herbaceous species, like tomato, differs from large tree crops.

3.4. Water use efficiency

Based on previous responses, no consensus can be achieved concerning the influence of KL on water use efficiency. While some studies have described increases in intrinsic water use efficiency (WUE$_i$) (Jifon and Syvertsen, 2003; Glenn et al., 2010; Correia et al., 2014; Boari et al., 2015; Brillante et al., 2016; Dinis et al., 2018), others have revealed an opposite trend (Glenn et al., 2003; Steiman et al., 2007; Roussos et al., 2010; Shellie and King, 2013; Brito et al., 2018c) or simply no influence of this variable (Denaxa et al., 2012). Similarly, instantaneous water use efficiency (A/E) was also increased (Glenn et al., 2010; Jifon and Syvertsen, 2003) or not affected (Nanos, 2015) by KL application. Moreover, the water use efficiency calculated based on yield/applied water was increased in tomato plants (Boari et al., 2016; Djurovića et al., 2016; AbdAllah, 2017), while was no affect in sweet pepper (Ćosić et al., 2015). By contrast, on the basis of biomass production/applied water, was improved in tomato plants (Boari et al., 2016; Djurovića et al., 2016), but it was not affected in olive trees (Brito et al., 2018c) and sweet pepper plants (Ćosić et al., 2015). In summary, due to the different variations in A, g_s and E, as well other processes such as the respiration rate, water use efficiency is affected in different ways by KL application, with stressful conditions serving as a determining factor. Moreover, the plant structure and its influence on the light distribution can also alter the whole-plant water use efficiency.

3.5. Leaf biochemistry and mineral composition

The influence of KL particles in leaf biochemistry has been minimally studied, with greater prominence having been given to the composition of photosynthetic pigments. Generally, KL prevents chlorophyll degradation (Glenn et al., 2003; Roussos et al., 2010; Correia et al., 2014; Nanos, 2015; Segura-Monroy et al., 2015; Brito et al., 2018c) and improves carotenoid concentrations under stressful conditions (Shellie and King, 2013; Correia et al., 2014; Dinis et al., 2016b; Brito et al., 2019). The reduction of the chlorophyll *a*/chlorophyll *b* ratio (Chl$_a$/Chl$_b$) (Shellie and King, 2013; Nanos, 2015; Brito

et al., 2018c) and increase in the total chlorophyll (Chl$_{(a+b)}$)/ carotenoids (Car) ratio (Shellie and King, 2013; Correia et al., 2014; Brito et al., 2018c) are also recognized effects of KL application, as well as typical features of low-light-adapted leaves Gregoriou et al., 2007; Lichtenthaler et al., 2007; Brito et al., 2018c). By contrast, the reduced Chl$_a$/Chl$_b$ ratio indicates that photosystems have larger antenna sizes at the expense of reaction centre pigment proteins to enhance their ability to capture and utilize photon energy (Gregoriou et al., 2007; Lichtenthaler et al., 2007), and the increased Chl$_{(a+b)}$/Car ratio indicates a reduced need for photoprotection of chlorophylls, as carotenoids play an important role in scavenging reactive oxygen species (ROS) and releasing the excess energy by thermal dissipation via the xanthophyll cycle (Lisar et al., 2012; Sharma et al., 2012).

Relative to glycometabolism, Brito et al. (2018c, 2019) observed starch depletion in KL-sprayed olive trees, indicating the use of carbohydrates reserves since starch is an important storage carbohydrate that is usually mobilized in the form of sugar (Rosa et al., 2009). Still, while young drought-exposed olive trees grown in pots containing KL induced an accumulation of total soluble sugars (Brito et al., 2018c), rainfed olive trees in the field showed a reduced accumulation of soluble sugars, indicating that newly assimilated carbon was exported (Brito et al., 2019). Moreover, KL enhanced the accumulation of carbohydrates in stems, which could have a profoundly positive effect on tree performance in the following year (Brito et al., 2019).

Moreover, some studies have demonstrated that KL generally reduces the oxidative damage in sprayed organs. In rainfed grapevines, a reduced accumulation of ROS (Dinis et al., 2016b) and lipid peroxidation (Bernardo et al., 2017) were found in sprayed leaves and berries, as well an increase in soluble proteins (Dinis et al., 2018). Conversely, in drought-exposed olive trees, despite higher ROS levels, reduced signals for oxidative stress in leaves, *i. e.,* reduced electrolyte leakage levels, and increased soluble proteins, total thiols and pigment concentrations, were evident. Moreover, upon rewatering, KL-sprayed leaves displayed a higher capacity to increase the total soluble protein levels (Brito et al., 2018c). Regarding antioxidant defence, while KL boosts the antioxidant defence system in grapevine (*e.g.,* increased phenolics, antioxidant capacity and activity of ascorbate-glutathione cycle key enzymes), in the olive tree, it reduces the necessity to invest in secondary metabolism (*e.g.,* reduced ascorbate, phenolics and total antioxidant capacity) (Brito et al., 2018c, 2019). The distinct responses might be due to the nature of each species and the tolerance level to stress, although in both species, KL improves the balance between ROS production and scavenging.

Regarding the plant ionome, the available information is even more limited. In apple trees, no significant influence of KL application was found in mineral composition (Al-Absi and Archbold, 2016); in olive trees, the most significative influence of KL was a reduction of the leaf N concentration during the summer (Brito et al., 2019). According to the latter authors, this phenomenon might be explained by an increased translocation of N from leaves to fruits, as fruits are an important sink of N in the initial phase of growth (Rodrigues et al., 2012) and KL displayed a higher yield (Brito et al., 2018d).

Despite the limited evidence, hormonal dynamics were also found to be modulated by KL application. A reduction of abscisic acid (ABA) and increase in indoleacetic acid (IAA) concentrations and immunohistochemical signals were observed in both grapevine (Dinis et al., 2018) and olive (Brito et al., 2019) leaves. Reduced ABA and increased IAA might reflect better conditions (lower temperature and better water status), leading to improved plant development (Dinis et al., 2018). Interestingly, in KL-sprayed olive leaves, the increased IAA signal in the main vascular tissues suggested the transport of IAA, and the increased signal detected in upper palisade parenchyma might be a response to the reduced irradiation incidence due to the kaolin particle film (Brito et al., 2019).
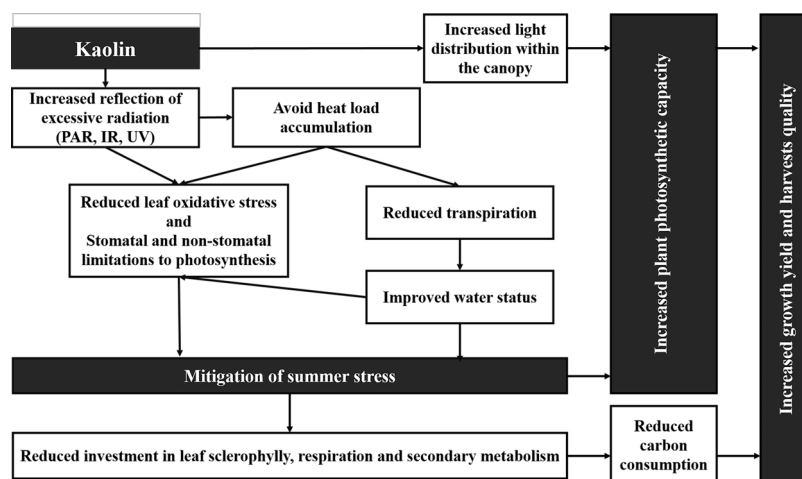
Fig. 2. Schematization of kaolin action on plants performance.

3.6. Growth and yield

Although KL generally exerts a positive influence on plant growth and/or biomass accumulation (Roussos et al., 2010; Javan et al., 2013; Segura-Monroy et al., 2015; Brito et al., 2019), the positive influence on yield is more recognized (Glenn et al., 2003; Saour and Makee, 2003; Cantore et al., 2009; Javan et al., 2013; Correia et al., 2014; Segura-Monroy et al., 2015; Boari et al., 2016; Djurovića et al., 2016; AbdAllah, 2017; Brito et al., 2018d). Still, some contradictory results might be found due to the influence of environmental conditions, species and cultivars and/or plant structure. For example, Boari et al. (2015) reported a decrease in growth and biomass accumulation in tomato, bell pepper and zucchini with optimum irrigation and an increase with deficient irrigation. By contrast, in olive trees cv. Cobrançosa, Brito et al. (2018c) found no significant influence on biomass accumulation in drought-exposed young potted plants, while Brito et al. (2019) recorded an increase in growth in rainfed field trees. Regarding yield, in grapevine, Brillante et al. (2016) reported distinct responses in relation to different harvest years, while Shellie and King (2013) found not significant influence in a different location. In olive trees in different locations, Nanos (2015) found no significant influence in cv. Konservolea, while Brito et al. (2018d) found an increase in yield of cv. Cobrançosa in response to KL application.

In tomato plants, KL mitigated the detrimental effects of increased salinity on both total and marketable yield (Boari et al., 2016), while under favourable water conditions, KL improved the marketable yield (Pace et al., 2007; Cantore et al., 2009) and decreased the unmarketable yield (Cantore et al., 2009).

3.7. Harvest quality

In general, the application of KL increases the harvest quality of the sprayed crops. In olive trees, an increase in fruit dry matter and oil content was reported, as well as an increase in the oxidative stability and shelf life of the extracted olive oil and a reduction of free acidity (Saour and Makee, 2003; Khaleghi et al., 2015; Nanos, 2015), although the absence of an effect on olive oil quality indices was also reported (Brito et al., 2018d). The influence on olives and olive oil phenolic compounds was more related to annual variations in weather than to KL application. While KL seamed to allow elevated production of these metabolites under mild summer conditions and/or to attenuate their degradation due to frost events, under severe summer conditions, it reduced the necessity to invest in secondary metabolism (Brito et al., 2018d). In apple trees, KL increased the postharvest fruit quality, reducing the loss of weight, soluble solids (SS) and titratable acidity (TA) after 70 days of storage storage (Ergun, 2012). In grapevine, KL

increased the concentrations of phenolics in berries, as well anthocyanins, ascorbate, and the antioxidant capacity (Shellie and King, 2013; Brillante et al., 2016; Conde et al., 2016; Dinis et al., 2016b), while the produced wines were visually judged to be more attractive and slightly more appreciated than those obtained without KL application (Brillante et al., 2016). Moreover, KL increased the redness colour of apple, mango and tomato (Glenn et al., 2003; Glenn, 2016; Pace et al., 2007; Chamchaiyaporn et al., 2013) and reduced sunburn damage in apple, pomegranate, sweet pepper and tomato fruits (Glenn et al., 2002; Wünsche et al., 2004; Vatandoost et al., 2014; Cosić et al., 2015; Boari et al., 2016). In sweet pepper KL modified the pepper mineral composition, increasing Ca, Na, and B and decreasing Al contents (Makus, 2005), but did not affect the sugar and organic acids content and antioxidant activity (Cosić et al., 2015). In tomato, KL was found to improve the lycopene content (Pace et al., 2007; Cantore et al., 2009; Boari et al., 2016) and total soluble solids (Boari et al., 2016), although no effects were recorded in terms of fruit chemical composition (Djurovića et al., 2016; AbdAllah, 2017).

4. Conclusions and future directions

The abiotic stresses alleviation induced by kaolin involves changes in important morphological, physiological and biochemical mechanisms. By improving radiation reflection, kaolin first avoids heat load accumulation, thereby reducing water loss through transpiration, while it maintains a relatively high stomatal conductance and improves the plant water status. Second, kaolin reduces leaf damage, directly by reducing the photodamage caused by excess excitation energy and indirectly by reducing oxidative stress, a result of reduced heat accumulation and better water status. Then, by alleviating the stomatal and non-stomatal limitations on photosynthesis and by increasing the light distribution within the canopy, kaolin allows better photosynthetic activity at the whole-plant scale. Additionally, water conservation, the cooler canopy and the shaded effect in KL-sprayed plants will likely reduce the investment in leaf sclerophylly and the total amount of carbon consumed during respiration and secondary metabolism, influencing the total carbon balance. Taken together, these changes induced an increase in growth, yield and even harvest quality (Fig. 2). However, the effectiveness of kaolin in mitigating the adverse effects of stress could be highly dependent on environmental conditions. It can be generally assumed that a greater effect occurs under moderately stressful conditions and may be compromised with stress prevalence and/or intensity. Moreover, this response is also highly variable according to the species or even genotype, and it is probably dependent on the light saturation point and shade-induced characteristic responses of leaves, especially over the long-term. The plant structure is also a

challenge, and kaolin provides a more advantageous effect in trees with denser canopies, which benefit from the light redistribution within the canopy.

The use of the kaolin reflective particle film in stress alleviation appears to be a promising strategy to implement in arid and semi-arid areas, where water availability is a rising problem and the incident PAR usually exceeds the capacity of plant use. This practice provides significant economic benefits, reducing the dependence on excessive and expensive irrigation to mitigate stress. However, it will be necessary to address how to optimize KL use, namely by increasing knowledge concerning the plant response to its application, identifying crops that could benefit from this technology, and determining the best time and frequency of applications. Moreover, studies examining the interactions of kaolin application with other agronomic practices, such as cover crops and deficit irrigation strategies, are needed to improve the effectiveness of KL under more severe stress conditions.

Acknowledgements

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